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Visual-motor Optimization in Binocular Control

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When we view objects at various depths, the 3-D rotations of our two eyes are neurally yoked in accordance with a recently discovered geometric rule, here called *the binocular extension of Listing's law*, or L2. This paper examines the visual and motor consequences of this rule. Although L2 is a generalization of Listing's original, monocular law, it does not follow from current theories of the latter's function, which involve minimizing muscle work or optimizing certain aspects of retinal image flow. This study shows that a new optimization strategy that combines stereo vision with motor efficiency does explain L2, and describes the predictions of this new theory. Contrary to recent suggestions in the literature, L2 does not ensure single vision of lines orthogonal to the visual plane, but rather reduces cyclodisparity of the visual plane itself; and L2 does not arise because a single, conjugate angular velocity command is sent to both eyes, but actually requires that the two eyes rotate with different speeds and axes when scanning an isovergence surface. This study shows that L2 is compatible with a 1-D control system for vergence alone (because horizontal and torsional vergence are yoked) and a 3-D system for combined, head-fixed saccades and vergence.

Eye movements Vergence Ocular torsion Binocular vision Listing's law Human

INTRODUCTION

The neural circuitry that steers our two eyes has been shaped by natural selection to serve stereo vision. But is this motor system optimized, in the sense of minimizing some physiologically important cost function? Given the basic facts of human visual-motor anatomy—namely that we have two eyes, each with a small disk-shaped fovea and each able to rotate with three degrees of freedom (horizontal, vertical and torsional)—what are the possible ways to position the eyes so that both foveae point at the same object, and what are the advantages of the particular pattern of coordination that we actually use?

It might seem that there is only *one* possible way to coordinate a pair of eyes, once we rule out chameleonism by requiring that both foveae point at a single target. In fact there are infinitely many distinct binocular configurations that are compatible with viewing any one target location. All these configurations point the two gaze lines at the target, but they differ in how the eyes are cyclorotated about their own lines of sight. From this infinity of possibilities, the brain chooses just one (Mok *et al.*, 1992). In other words, for any target location, there is a unique binocular configuration that is actually used to fixate it (when the target is stationary and the head is still and upright).

In the special case where the visual target is at optical infinity, the law describing the actual pattern of eye positions has been known for more than a century (Helmholtz, 1867). Listing's law states that if e is any position actually taken up by the eye, then there is a plane, called the velocity plane (or displacement plane) of e, such that the eye adopts only those orientations that can be reached from e by a single rotation about an axis lying in the plane. Velocity planes associated with different eye positions e are distinct, and are rotated relative to one another. There is a unique eye position p with the property that the velocity plane associated with p is orthogonal to the line of sight in position p. Helmholtz named this unique eye position the "primary position", and its velocity plane "Listing's plane".

A little more terminology now will simplify the impending discussion of vergence kinematics. First of all, we give p a new name, p^0, and call it the "zero-vergence primary position". What Helmholtz called Listing's plane now becomes the "zero-vergence Listing's plane", LP^0. And finally, in a very useful bit of nomenclature, we call the velocity plane of p^0 the "primary plane". Notice the distinction: LP^0 is the velocity plane of p^0 when vergence is zero, whereas the primary plane is the velocity plane of p^0, period. Thus the primary plane coincides with LP^0 when vergence is zero but, as we shall see shortly, it rotates away from LP^0 when the eyes converge, which means that each eye then

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moves toward and away from its p^0 by turning about axes lying in its rotated primary plane, not in LP^0. The advantage of the primary plane concept—as compared with Listing's plane—is that it allows us to discuss vergence kinematics without having to change the reference eye positions with respect to which eye orientations are expressed; we can express eye orientations relative to p^0 whatever the current state of vergence.

Equipped with this vocabulary, we can now consider what happens when the visual target looms up close to the subject's face. The first observation is that Listing's law fails, as Allen found in 1954 (Allen, 1954). The full kinematic pattern was revealed when Mok *et al.* (1992) measured eye orientations of subjects viewing isovergence surfaces, which are concave forms, precisely shaped and positioned so that wherever the subject looks on the surface, the angle between the two lines of sight is always the same; for example, if a subject binocularly fixates a target point located anywhere on the 40 deg isovergence surface, then the angle between the lines of sight must be 40 deg. The pattern Mok *et al.* (1992) reported will be referred to here as "the binocular extension of Listing's law", abbreviated L2:

When the eyes are converged D°,

the primary plane of each eye is turned temporally (L2)

through the angle μD°

where μ is a constant and D is the disconjugate, or vergence, angle. This means that when you converge your eyes so that the angle between your lines of sight is 40 deg, your primary planes swing out like saloon doors, pivoting $\mu \times 40$ deg about the ocular centres; e.g. if $\mu = \frac{1}{4}$ then each primary plane rotates 10 deg. Actually, Mok *et al.* (1992) found that $\mu \approx \frac{1}{6}$, meaning that the primary planes turned, on average, only $\sim D/6$ deg, but for theoretical reasons the authors regarded the angles as tending toward an ideal value of $D/4$ deg, like vestibulo-ocular reflex gains tending toward -1. In contrast, Van Rijn & Van den Berg (1993) found angles of almost $D/2$ deg. Van Gisbergen & Minken (1994), who set out to resolve the discrepancy, found values close to $D/4$ deg under a variety of visual conditions. Thus all groups agree that the eyes' rotation axes remain confined to planes for any vergence angle, and that these planes rotate temporally and symmetrically as the eyes converge, but different groups disagree on the angles of rotation. I shall return to this controversy below.

Note that L2 is a generalization of Listing's law, and reduces to it when the vergence angle $D = 0$. Many theories, most dating in their essentials to the mid-19th century, have been proposed to explain Listing's law by identifying the variables that it optimizes (e.g. Fick, 1858; Wundt, 1859; Helmholtz, 1867; Hering, 1868). Do any of these theories account for L2?

METHODS

This paper uses computer simulations to explore the consequences of various quantitative theories of binocular coordination. Here I define the most important mathematical terms arising in these theories. Detailed equations for the computer simulations and visual-motor theorems are in the Appendix.

Two different coordinate systems will be used to describe three-dimensional eye orientations. In Helmholtz coordinates, an eye position is decomposed into a sequence of three rotations starting from a reference position in which the line of sight points straight ahead. First is a vertical rotation through an angle V about a transverse axis (parallel with the interaural line in reference position), second a horizontal rotation through an angle H about an axis that is vertical with respect to the eye, and third a torsional rotation through an angle T about the line of sight. The angles V, H and T are the vertical, horizontal and torsional Helmholtz coordinates of the eye position. Positive directions for these angles will be downward, leftward and clockwise (from the subject's viewpoint), respectively, to agree with the usual right-handed conventions for quaternions (Tweed & Vilis, 1987) and rotation vectors (Haustein, 1989). An alternative, equivalent definition of the Helmholtz angles, which will be useful in deriving Eq. (3) below, is expressed in terms of head-fixed rather than eye-fixed axes: we apply first a torsional rotation through an angle T about an axis parallel with the nasooccipital line, second a horizontal rotation through an angle H about an axis that is vertical with respect to the head, and third a vertical rotation through an angle V about an axis parallel with the interaural line. An important fact about Helmholtz coordinates is that, if the two eyes are to foveate the same object, then the Helmholtz-vertical angles of the right and left eyes must be equal (Helmholtz, 1867; Van Rijn & Van den Berg, 1993):

$$V_R = V_L \tag{1}$$

For comparison with experimental data, eye positions will also be expressed in quaternion coordinates. A quaternion q has four components and may be regarded as the sum of a scalar component q_0 and quaternion vector $\mathbf{q}$; i.e., $q = q_0 + \mathbf{q}$. If we define a quaternion q by these equations:

$$q = q_0 + \mathbf{q} = \cos(\varepsilon/2) + \mathbf{n}\sin(\varepsilon/2). \tag{2}$$

where $\mathbf{n}$ is a three-component vector of length 1, then q represents a rotation through angle ε about an axis parallel with $\mathbf{n}$. The vector $\mathbf{n}$ is oriented along the rotation axis according to the right-hand rule: if you point your right thumb in the direction of $\mathbf{n}$, your fingers curl round in the direction of the rotation. If this rotation q began with the eye in its "zero", or reference, position, then the angle ε is called eye eccentricity, because it measures how far the eye has rotated away from reference. Quaternion algebra is described in Westheimer (1957), Tweed & Vilis (1987), and in many general kinematics and mechanics texts such as Brand (1948), Hestenes (1986) and McCarthy (1990).

Converting between Helmholtz coordinates and quaternions is relatively painless. For example, to find the quaternion q that is equivalent to a set of Helmholtz

coordinates, multiply the quaternions corresponding to the individual V, H and T rotations. Thus $q = (c_{V/2} + \mathbf{j}s_{V/2})(c_{H/2} + \mathbf{k}s_{H/2})(c_{T/2} + \mathbf{i}s_{T/2})$, where $c_{V/2}$ is the cosine of half the Helmholtz-vertical coordinate, $s_{H/2}$ is the sine of half the Helmholtz-horizontal coordinate, etc.; and **i**, **j** and **k** are (head-fixed) unit vectors pointing along the coordinate axes: forward, left and up. This works out to:

$$q_0 = (c_{V/2}c_{H/2}c_{T/2} - s_{V/2}s_{H/2}s_{T/2}) \quad (3a)$$

$$\begin{aligned}\mathbf{q} = {} & \mathbf{i}(c_{V/2}c_{H/2}s_{T/2} + s_{V/2}s_{H/2}c_{T/2}) \\ & + \mathbf{j}(c_{V/2}s_{H/2}s_{T/2} + s_{V/2}c_{H/2}c_{T/2}) \\ & + \mathbf{k}(c_{V/2}s_{H/2}c_{T/2} - s_{V/2}c_{H/2}s_{T/2})\end{aligned} \quad (3b)$$

To express eccentricity ε in terms of Helmholtz coordinates, use Eq. (3a), together with the fact that $q_0 = \cos(\varepsilon/2)$ [from Eq. (2)] to give

$$\varepsilon = 2\cos^{-1}(c_{V/2}c_{H/2}c_{T/2} - s_{V/2}s_{H/2}s_{T/2}) \quad (4)$$

In the Discussion we briefly encounter a third coordinate system, Fick's, which decomposes an eye position into three rotations just as Helmholtz's does, except that the sequence of rotations is different: first horizontal, then vertical, then torsional, about eye-fixed axes. The angles F_H, F_V and F_T of these rotations are the horizontal, vertical and torsional Fick coordinates of the position.

RESULTS

Listing's law is not necessary to reduce degrees of freedom

It is sometimes suggested that the purpose of Listing's law is to reduce the degrees of freedom of eye motion, from three down to two, in order to simplify motor control. But there are many other ways, besides Listing's law, of reducing freedom. For example, if the eye moved in a way that held the Helmholtz-torsional coordinate (defined in Methods) fixed at zero then Listing's law would be violated [this is proven in Eq. (6) below], but the eye would still be restricted to two degrees of freedom. Whenever the eye is constrained to two degrees of freedom, we shall say that Donders' law holds. Listing's law, then, is a special case of Donders' in which eye positions are confined by velocity planes, and so a complete explanation of Listing's law must identify the specific advantage of having these planes. Another problem with the degrees of freedom explanation is that it does not go deep enough. We can still ask: what is the real advantage of restricted freedom? Does it simplify motor control, or might it be reducing muscle work, or streamlining visual information processing, or serving some other purpose? In what follows we examine the possibilities.

A motor theory

The oldest living theory of Listing's law, put forward by Fick and Wundt (see Helmholtz, 1867), holds that it enhances motor efficiency by minimizing the rotational eccentricity of the eye. A modern mathematical formulation is given by Hepp (1990). The theory is based on the fact that some eye rotations are more efficient than others when it comes to moving the gaze line. For example, if an eye rotates x deg around an axis that is orthogonal to the gaze line, then that line swings through an angle of x deg as well. This is the best ratio of gaze rotation to eye rotation that can be achieved. At the other extreme, if the eye rotates x deg about an axis that is parallel with the gaze line, then the line does not move at all. Other axes of eye rotation yield intermediate ratios of gaze rotation to eye rotation; (in fact the ratio, for infinitesimal rotations, is $\sin\theta$, where θ is the angle between the axis and the gaze line).

Now suppose there is some "special", central eye position and that we want to direct our gaze in all directions using the smallest possible rotational displacement from centre; i.e. with the smallest possible 3-D eye eccentricity ε [Eq. (4)]. Clearly, the way to do this is always to move the gaze line as efficiently as possible, by rotating the eye to and from centre about axes orthogonal to the vector $\mathbf{g}_c$, which is the gaze direction in centre position. That is, adopt only those positions that can be reached from centre by rotating about an axis in the plane orthogonal to $\mathbf{g}_c$. If we rename the centre position *primary position* and call the plane *Listing's plane*, we see that we have derived Listing's law as a consequence of minimizing eccentricity. (See Hepp, 1990, for an algebraic proof.)

But why is it valuable to minimize eccentricity? One possibility has to do with muscle work. We know that there is an elastic force in the orbit that tries to pull the eye back toward a rest position, and that this force increases with the rotational eccentricity of the eye. Let us assume that it is this elastic force rather than, say, viscous force which is the major factor determining muscular effort—a reasonable assumption given that the eye spends more time holding still or moving slowly than moving fast. Then minimizing rotation away from rest position will also minimize the elastic restoring force and, therefore, the exertion required to maintain the eccentric position. Thus, the motor theory shows how Listing's law might follow from a strategy that maximizes metabolic energy efficiency.

More importantly, perhaps, minimizing eye eccentricity also brings the eye the same advantage that staying near centre court brings a tennis player, namely swift and flexible responses to incoming stimuli. I shall refer to this functional advantage of minimizing eccentricity as the "centre-court principle".

Several minor objections and revisions can be made to Fick and Wundt's theory, but its major flaw is that it cannot explain L2. If the eyes were orienting themselves so as to achieve the desired gaze direction with the least eye eccentricity, each eye would always use the same, minimum-eccentricity orientation whenever it looked in any given direction: the orientation of each eye would depend only on its own gaze direction and not, for example, on what the other eye was doing. Mok and colleagues' discovery that the primary planes rotate

temporally when the eyes converge shows that each eye actually adopts different orientations to look in the same direction, depending on vergence. Thus, some factor other than eye eccentricity must be playing a role.

Monocular visual theories

Discussing Fick and Wundt's principle of motor efficiency, Helmholtz wrote that "Probably it is actually fulfilled in the real normal movements that are made by the eyes. But I did not think I could venture to accept this principle as final" (Helmholtz, 1867, p. 70). Helmholtz felt that the ultimate explanation of Listing's law would have to identify some advantage that it brings to vision. He devised a visual theory, and unfortunately dubbed it the "principle of the easiest orientation", a name which has misled many skimmers of his work into believing, falsely, that his theory was essentially motor, like Fick and Wundt's.

Helmholtz's theory is explained in detail by its author (Helmholtz, 1867) and by Hepp (1995). Here it will suffice to say that it, like another hypothesis proposed by Hering (1868), views Listing's law as optimizing certain aspects of image flow across the retina, thereby simplifying the neural processing of visual information. Unfortunately, these two theories do no better than Fick and Wundt's at predicting the temporal pivoting of the primary planes during vergence.

There is an additional, reference-frame problem with theories like Helmholtz's and Hering's that are based on retinal image flow. Retinal flow depends on the eye's motion relative to a space-fixed reference frame, not its motion relative to a head-fixed frame, because most objects we see are, fortunately, anchored in space rather than to our heads. So if the goal is to optimize retinal image flow, it should be the eye's rotation relative to *space* that obeys Listing's law. In other words, Helmholtz's and Hering's explanations for Listing's law assumed that it governs the eye's motion in space. In fact, recent data have shown that it is eye rotation relative to the head that follows Listing's law, whereas, owing to head movement, eye rotation relative to space does not (Glenn *et al.*, 1992; Hepp, 1995; Radau *et al.*, 1994). When a human subject looks 30 deg down and 60 deg right, using a natural combination of eye and head motion, the eye in space typically breaks Listing's law by a flagrant 12 deg (Radau *et al.*, 1994).

Given these objections, then, I think the main purpose of Listing's law and L2 is likely not to optimize the absolute motion of retinal images of space-fixed objects, as proposed by Helmholtz and Hering. However, as we shall see, L2 may still optimize the motion of a retinal image *relative* to the motion of the corresponding image on the other retina.

Binocular vision

Do we coordinate our eyes so as to optimize, in some sense, the correspondence between the images on the two retinas? Geometry dictates that no binocular coordination strategy can yield perfect correspondence, eliminating

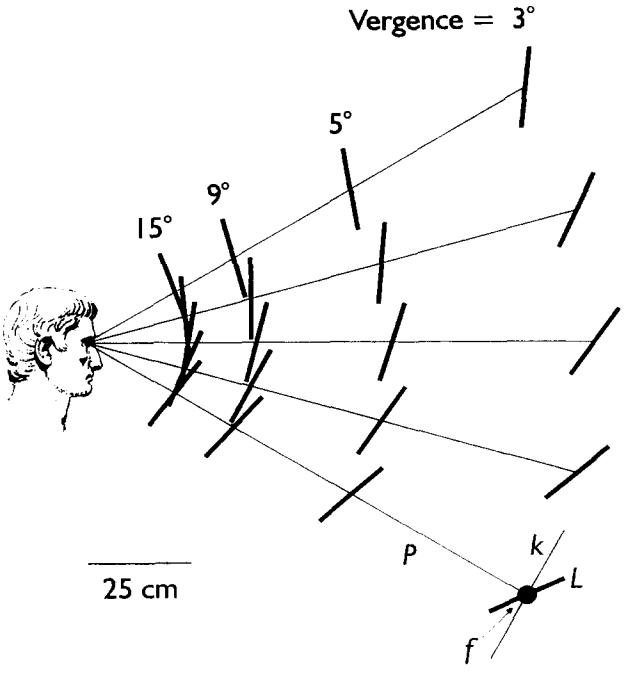

FIGURE 1. Influence of L2 on the vertical horopter. Any line k through fixation point f and orthogonal to visual plane P casts its images on the vertical meridians of both retinas. But k is nevertheless seen double, because the vertical meridians are not "corresponding lines". Corresponding "vertical" meridians in the two retinas tilt ~2 deg away from each other when both eyes look straight ahead, with the result that the line L, the vertical horopter, is seen single. This simulation shows how L2 with $\mu = \frac{1}{4}$ causes L to tilt for different fixation points.

double vision throughout the visual field (Van Rijn & Van den Berg, 1993). The best that can be achieved is to keep the most important elements in the field in register. But what are these elements? In an excellent recent analysis of vergence strategies, Van Rijn & Van den Berg (1993) showed that one consequence of L2, with $\mu = \frac{1}{4}$, is that the Helmholtz-torsional coordinates (defined in Methods) of the two eyes are equal:

$$T_R = T_L \tag{5}$$

(Actually L2 with $\mu = \frac{1}{4}$, as I defined it in the Introduction, does not ensure that the Helmholtz-torsional coordinates are always precisely equal, but the difference is very small; e.g. less than 0.4 deg when vergence is 30 deg and both gaze lines are within 40 deg of straight ahead.)

Van Rijn and Van den Berg inferred that obeying Eq. (5) would ensure single vision of lines orthogonal to the visual plane, which is the plane containing the gaze lines of both eyes (defined in Helmholtz, 1867). For example, if you look at the horizon with your head upright, your visual plane is earth-horizontal, and therefore trees, and other lines orthogonal to the horizon plane, should be seen without cyclodisparity.

Surprisingly, this inference about cyclodisparity is incorrect, for the reason illustrated in Fig. 1. Here, the line k passes through the fixation point f and is orthogonal to the visual plane P. As long as Eq. (5) holds, this line k

casts its images on the vertical meridians of both retinas, as Van Rijn and Van den Berg calculated. But k is nevertheless seen double, because the vertical meridians are not "corresponding lines", as can be shown by psychophysical experiments (Helmholtz, 1867; Ogle, 1950). Corresponding "vertical" meridians in the two retinas are excyclorotated ~ 2 deg away from each other when both eyes look straight ahead, with the result that the line L in Fig. 1, tilted back from k, casts its two images on the corresponding meridians. Therefore, it is L, and not k, that is seen single (Helmholtz, 1867; Ogle, 1950). This line L is called the vertical horopter (Howard, 1982), or the midsagittal section through the vertical line-horopter (Helmholtz, 1867). The angle between L and k depends on the orientations of the corresponding vertical meridians, which in turn depend on ocular torsion. If we assume that the eyes obey L2 with $\mu = \frac{1}{4}$, then the simulation in Fig. 1 shows how the vertical horopter will tilt for different fixation points. For details of this simulation, see the Appendix (*Vertical horopter*).

Given that Eq. (5) does not, in fact, ensure single vision of lines orthogonal to the visual plane, what are its true perceptual consequences? Perhaps the most important consequence is that the visual plane itself will be seen with no, or at most very little, cyclodisparity (see Appendix: *Helmholtz torsion*). The special role of the visual plane in space perception is considered in the Discussion.

The second criterion

Unfortunately, aligning the images of the visual plane [by satisfying Eq. (5)] cannot be the sole purpose of L2, because many other patterns of binocular coordination besides L2 would achieve that goal just as well. For example, if both eyes rotated as if mounted on Helmholtz gimbals, with their Helmholtz-torsional angles both fixed at zero, Eq. (5) would be satisfied and the images of the visual planes would stay aligned. This possibility is of special interest because it is the *only* way to move the eyes so that the images of the visual plane are not just aligned, but always fall on the same horizontal meridian of each retina. Thus, if human retinas retained some remnant of the horizontal, foveal streak found in rabbits and other animals, this would be the strategy that would keep the image of the visual plane on the foveal streak. But this strategy would violate L2. To see this, note that Listing's law, which is a consequence of L2, requires that $q_T = 0$. By Eq. (3a), $q_T = c_{V/2}c_{H/2}s_{T/2} + s_{V/2}s_{H/2}c_{T/2}$, and so Listing's law says that $c_{V/2}c_{H/2}s_{T/2} = -s_{V/2}s_{H/2}c_{T/2}$. Divided through by $c_{V/2}c_{H/2}c_{T/2}$, this simplifies to

$$\tan(T/2) = -\tan(V/2)\tan(H/2) \qquad (6)$$

which cannot be satisfied if T is fixed at zero. Therefore a system that keeps Helmholtz torsion T equal to zero disobeys Listing's law [Eq. (6)] and hence L2, despite satisfying Eq. (5).

Some additional performance criterion, beyond Eq. (5), must therefore be operating to produce L2. Theoretical arguments suggest that this second criterion is not sensory but motor. In brief, the argument is that

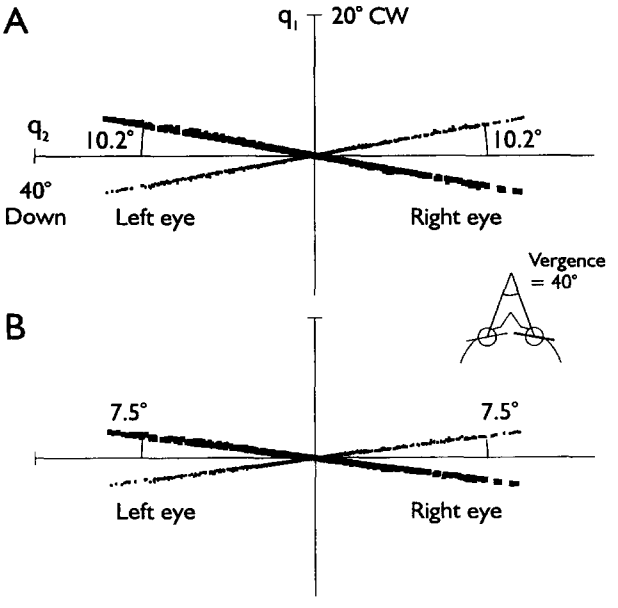

FIGURE 2. A visual-motor strategy yields L2. (A) Computer simulation of a strategy that minimizes eye eccentricity [Eq. (7)] while holding the Helmholtz-torsional coordinates of the two eyes equal [Eq. (5)]. Quaternion vectors of eye position are seen from above the simulated subject, whose vergence angle is 40 deg. As required by L2, these quaternion vectors lie in temporally rotated planes. Each plane is rotated 10.2 deg, implying a μ of 10.2/40, or 0.255, which is close to the values found experimentally by Van Gisbergen & Minken (1994). (B) If equality of Helmholtz torsion [Eq. (5)] is not an absolute constraint, but is part of a weighted cost function (VM*), then the quaternion vectors still lie in temporally rotated planes, but the ratio, μ, of plane rotation to vergence angle can be $<\frac{1}{4}$.

monocular sensory effects are unlikely to account for L2, because most such effects depend on ocular motion relative to space and, as argued above, such motion does not obey L2, or indeed any positional constraint (Glenn *et al.*, 1992; Hepp, 1995; Radau *et al.*, 1994). Binocular criteria, on the other hand, usually constrain the motions of the two eyes relative to one another (e.g. requiring that their Helmholtz-torsional coordinates be equal) but not their motion relative to the head (e.g. specifying what the common Helmholtz-torsional angle is). Thus with monocular and binocular sensory factors ruled out, we are left with motor constraints as the likely second source of L2.

Visual-motor theory

Perhaps the most promising motor constraint is Fick and Wundt's criterion that eye eccentricity ε [i.e., total rotational displacement from centre orientation in all three dimensions—Eq. (4)] be minimized. That is, the eyes should twist about their own lines of sight in such a way as to minimize 3-D eye eccentricity while still maintaining fixation on the visual target and satisfying Eq. (5). The proposal, then, is to combine Fick and Wundt's motor theory with Van Rijn and Van den Berg's Eq. (5). It will be shown that this combined visual-motor strategy—aligning images of the visual plane and

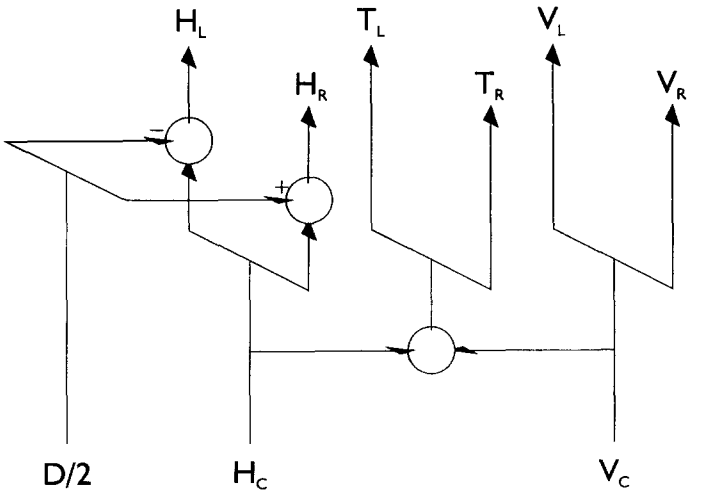

FIGURE 3. Flow diagram for a Helmholtz-coordinate model of binocular control, implementing Eq. (8).

minimizing ocular eccentricity—uniquely determines the positions of both eyes and agrees with L2.

Figure 2(A) shows a computer simulation of this strategy. The simulation does not minimize the eccentricity e [defined in Methods, Eq. (4)] of either eye alone, but the sum of the squared eccentricities of the two eyes:

$$\varepsilon_R^2 + \varepsilon_L^2 \tag{7}$$

Squaring is appropriate here because, for one thing, muscle work is most likely a roughly quadratic function of eye eccentricity, i.e., a nonlinear, upward-curving function. More importantly, exponents of ~ 2 are most suitable for quantifying the centre-court principle (see section entitled: *A motor theory*, above), because the distance a tennis player (or an eye) has to move to reach a target position, integrated over all possible target positions, varies with the squared eccentricity of the starting position. However, in any case, it appears that changing the exponents over a range of ~ 1–3 does not substantially affect the theory's predictions. In Fig. 2, the simulation is presented with targets over a ± 30 deg range horizontally and vertically, with vergence constant at 40 deg, and for each target it computes the unique binocular configuration that aims both foveas at the target and satisfies the following condition, which defines what shall be called the "visual-motor theory" (VM):

$$\text{Minimize } \varepsilon_R^2 + \varepsilon_L^2 \text{ subject to } T_R = T_L \text{ (VM)}$$

For comparison with experimental data, the eye positions are expressed as quaternion vectors $\mathbf{q}$ (see Methods) in Fig. 2(A). The above view of the vectors in Fig. 2(A), plotting components q_1 and q_2, shows that they are arranged in symmetrically, temporally rotated planes as required by L2. Each plane is turned 10.2 deg, implying a μ of $10.2/40 = 0.255$, which is very close to the values measured by Van Gisbergen & Minken (1994), and not far from those found by Mok *et al.* (1992). Thus, the visual-motor theory yields L2, and with a reasonable value for μ. Using exponents of 1 or 3, instead of 2, in the simulation preserves the symmetry and magnitudes of the primary plane rotations, but the standard deviation of the scatter about the planes increases from ~ 0.1 to ~ 0.6 deg.

Figure 2(B) shows how a slight generalization of the visual-motor theory yields L2 with μ values less than 0.255. Here, the simulation has been altered so that equality of Helmholtz torsion [Eq. (5)] is no longer an absolute constraint, but is part of a weighted cost function to be minimized. Precisely, this extended visual-motor theory (VM*) is defined by the rule:

$$\text{Minimize } \alpha(\varepsilon_R^2 + \varepsilon_L^2) + (T_R - T_L)^2 \text{ (VM*)}$$

where α is a constant weighting factor. Setting $\alpha < 1$ yields $\mu \approx \frac{1}{4}$, while $\alpha = 3$ [shown in Fig. 2(B)] preserves the planarity, turning directions, and midline symmetry of Fig. 2(A) but reduces μ to 0.188, so that the turning angle is 0.188×40 deg $= 7.5$ deg. Thus the extended visual-motor theory can yield a range of μs, from 0 up to 0.255, at the cost of an extra parameter, α, which quantifies the relative importance of minimizing eccentricity vs holding the Helmholtz-torsional angles of the eyes equal. Details of both simulations in Fig. 2 are given in the Appendix: *Visual-motor simulations*. Because the original and extended visual-motor theories, VM and VM*, are qualitatively alike in most of their implications, I shall usually speak simply of the "visual-motor theory" in what follows, without distinguishing versions unless it makes a difference quantitatively, as when a calculation or simulation is being described.

Models

The visual-motor theory is meant to explain *why* L2 is obeyed. The next question is *how* the law might be implemented by the brain. Behavioral and electrophysiological findings suggest that the eyes are driven by a "cyclopean" neural command, identical for the two eyes.

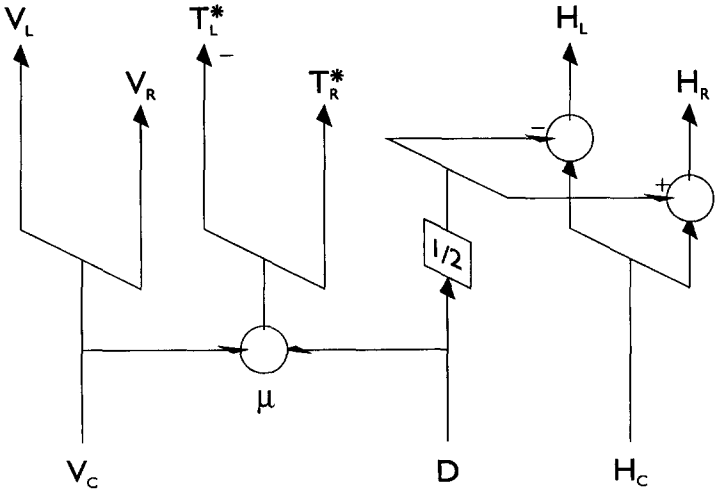

FIGURE 4. Flow diagram for a T^*-coordinate model of binocular control, implementing Eq. (11).

and a separate disconjugate command (Hering, 1868; Mays, 1984; Mays *et al.*, 1986; Schor, 1979). One simple model of this form has the eyes driven by two cyclopean vertical and horizontal commands, V_C and H_C, and a disconjugate command D, which are transformed by the final common path into Helmholtz coordinates for the right and left eyes according to the equations:

$$V_R = V_L = V_C,\ H_R = H_C + D/2,\ H_L = H_C - D/2,$$

$$T_R = T_L = -2\tan^{-1}\left(\tan\frac{V_c}{2}\tan\frac{H_c}{2}\right) \approx -V_C H_C/2 \quad (8)$$

In this model, illustrated in flow diagram form in Fig. 3, a single vertical command V_C is sent to both eyes. The horizontal commands to the right and left eyes, H_R and H_L, are simply the conjugate horizontal command H_C plus or minus half the disconjugate angle D. A single torsional command, derived from the H_C and V_C signals, is sent to both eyes. Note the importance of the coordinate system: when we obey L2 with $\mu = \frac{1}{4}$, the torsional components of the two eyes in quaternion coordinates can be very different, because the primary planes are not parallel; but the Helmholtz-torsional coordinates of the eyes are always equal. Thus, if the system works in Helmholtz coordinates, only a single torsional command is needed. Similarly for the vertical commands: the quaternion-vertical coordinates of the two eyes can differ, but the Helmholtz-vertical coordinates must be equal if the gaze lines are to intersect.

The model in Fig. 3 obeys L2 with $\mu = \frac{1}{4}$. What if we want a model where $\mu \neq \frac{1}{4}$? Interestingly, we can obtain flexible μ values without complicating the wiring diagram in Fig. 3 if we introduce a new coordinate system, which I shall call the T^* system. Here the vertical and horizontal coordinates are identical to the Helmholtz angles H and V, while the torsional coordinate is defined by:

$$T^* = T + VH/2 \quad (9)$$

Combining Eqs (8) and (9) we find that, in these new coordinates, the conditions for Listing's law and L2 are simply:

$$\text{Listing's law}: T^* = 0 \quad (10a)$$

$$\text{L2}: T_R^* = \mu DV,\ T_L^* = -\mu DV \quad (10b)$$

where T_R^* and T_L^* are the torsional coordinates of the right and left eyes. Like Eq. (5), these equations only approximately agree with Listing's law and L2 as defined in the Introduction, but again the approximations are very good. Comparing Eqs (8) and (10), notice again how the same law looks different when viewed through the lens of a new coordinate system. With Helmholtz coordinates, L2 appears as a rule that sets ocular torsion as a function of vertical and cyclopean horizontal eye position, independently of vergence [Eq. (8)]. With T^* coordinates, L2 sets ocular torsion as a function of vertical position and vergence, independently of cyclopean horizontal position [Eq. (10b)]. By modifying Eq. (8) so that the outputs are in T^* coordinates instead of Helmholtz coordinates, we obtain a new model:

$$V_R = V_L = V_C,\ H_R = H_C + D/2,\ H_L = H_C - D/2,$$

$$T_R^* = \mu DV_C,\ T_L^* = -\mu DV_C \quad (11)$$

Figure 4 is the flow diagram for this model. Its main advantage over Fig. 3 is that it allows us, by adjusting the gain of the node that multiplies D and V_C, to model L2 with different values of μ. And once again, I emphasize the different aims of these models vs the visual-motor theories. The models are suggesting neural mechanisms for L2, whereas the visual-motor theories are trying to explain *why* L2 arose. But there is a natural pairing between the models and the optimization theories. The Helmholtz-coordinate model in Fig. 3 agrees with the original version of the visual-motor theory, because both require that $\mu \approx \frac{1}{4}$; and the T^*-model in Fig. 4 fits in with the extended visual-motor theory, because both of these

allow more flexible values of μ. But in this case, the model is actually more flexible than the optimization theory. While the extended visual-motor theory can explain μ values only up to $\sim\frac{1}{4}$, the T^*-model can be set up to generate arbitrary μs.

DISCUSSION

We have seen that the visual-motor theory explains L2, but might there not be other theories that account just as well for the data? One proposal was discussed by Mok *et al.* (1992). They pointed out that symmetrical $x/4$ deg rotation of the primary planes is precisely what is needed to keep the velocity planes of the two eyes—the planes containing the angular velocity vectors—parallel during saccades or pursuit across any isovergence surface, assuming that the planes are parallel when the targets are at infinity.

But the fact that L2 with $\mu = \frac{1}{4}$ keeps the velocity *planes* parallel does not imply that the eye velocity vectors themselves are kept parallel or equal in magnitude, and in fact they are not: to obey L2 while tracking a point moving across an isovergence surface, the two eyes would sometimes have to rotate at different speeds and about different axes (see Appendix: *Binocular pursuit*). For example, if $\mu = \frac{1}{4}$ then even for vergence angles <30 deg the difference in speeds would amount to 15% under some conditions, and the angle between the instantaneous rotation axes of the two eyes would reach ~ 9 deg. Conversely, if the eyes *did* rotate with the same angular velocity, not only would they violate L2, but one or the other line of sight would break contact with the visual target, and in fact the lines of sight might fail to intersect at all.

This is a problem for the velocity-plane theory of Mok *et al.* (1992) as an explanation for L2, because no one has identified any advantage in keeping the velocity planes of the two eyes parallel, if the velocity vectors themselves are neither parallel nor equal in size. Moreover, the theory is somewhat embarrassed by the finding that, for many subjects, the Listing's planes of the two eyes are not parallel when the subject looks to infinity (Ferman *et al.*, 1987), which implies that the velocity planes are also not parallel. In contrast, the visual-motor theory still applies in subjects whose Listing's planes are not parallel; the only difference is that the primary planes are not symmetrically rotated as in Fig. 2(A), but inherit the asymmetry of the Listing's planes.

Thus the velocity-plane idea is not likely to explain L2. And as no other contender is currently in the field, we are left with the visual-motor theory—minimize a weighted sum of ocular eccentricity and the torsional disparity of images of the visual plane—as the only extant optimization rule that may account for the 3-D geometry of binocular coordination. The following sections examine further aspects of this theory and deliver predictions to be tested.

Visual tests for μ

As described above, different laboratoriess disagree over the value of μ, the ratio of primary plane rotation to the vergence angle. For unknown reasons, estimates for μ differ widely, with the three labs who have studied L2 reporting values of $\sim\frac{1}{6}$, $\sim\frac{1}{4}$ and nearly $\frac{1}{2}$. And as we have seen, the outcome of this debate matters for the visual-motor theory, which can explain μ values ranging from 0 to $\sim\frac{1}{4}$, but not higher. In a recent effort to resolve the controversy, Somani *et al.* (1996) brought in a new experimental technique. Whereas all previous studies used search-coil recordings of eye position to assess μ, Somani *et al.* obtained independent measures using psychophysical, visual tests. Their results indicated μ values between 0.15 and 0.22, in close agreement with the visual-motor theory and the earlier findings of Mok *et al.* (1992) and, slightly less close, with Van Gisbergen & Minken (1994) and Minken & Van Gisbergen (1994).

One of these visual tests can be adapted for home use, allowing you to check your own μ value in the comfort of your living room. You sit facing a wall so that the edge where wall meets ceiling is ~ 30 deg up and parallel with your interaural line. Hold one finger close to your face and high up, and fixate its tip, looking up with both eyes and keeping your head facing straight-forward. Position your finger so that the blurred image of the wall–ceiling edge runs through the fingertip in the background. That edge now lies in your visual plane, so if you see only a single image of it, your μ is close enough to $\frac{1}{4}$ to allow visual fusion (or you are suppressing one eye's image). If the right eye's image is rotated counterclockwise relative to the left eye's, then your μ is less than $\frac{1}{4}$, as in Fig. 2(B) and as reported by Mok *et al.* (1992) and Somani *et al.* (1996). If the right eye's image is clockwise relative to the left's, your μ is greater than $\frac{1}{4}$, as reported by Van Rijn & Van den Berg (1993).

Why align images of the visual plane?

This central question remains open: what is the functional advantage of eliminating or reducing cyclodisparity of images of the visual plane? The first thing to notice is that, *if* we assume that it is valuable to have *some* plane P that is seen edge-on without cyclodisparity, perhaps as a sort of landmark for spatial vision, and if this plane is to pass through the fixation point, then P must be the visual plane. To see this, note that P must contain the line of sight of each eye, because otherwise it would not be seen edge-on in that eye. But then P contains both lines of sight, and must therefore coincide with the visual plane (except in the special case where the gaze lines are parallel, in which case infinitely many different planes can be seen edge-on and aligned in both eyes). In other words, the visual plane is always seen edge-on by both eyes, and it is the only plane that is seen this way (except, again, when the gaze lines are parallel). So if you want to align the edge-on images of some plane, your only choice is the visual plane.

How might the visual plane serve as a landmark for spatial vision? One possibility has to do with judging line orientations. At least since Helmholtz's time it has been known that when a line is viewed binocularly, the

torsional disparity of its two images provides information about its orientation (cf. Helmholtz, 1867; Howard, 1982). For example, if a line in the midsagittal plane is close to your face with its top end tilting toward you, then the right eye's image of the line will be rotated counterclockwise relative to the left eye's. If the top of the line is tilting away from you—to be precise, it must be tilting away more than the vertical horopter, as shown in Fig. 1—then the torsional disparity will be reversed, with the right eye's image rotated clockwise relative to the left eye's.

Unfortunately, torsional disparity also depends on the tilt of the eyes: their cyclotorsion relative to one another. If the right eye suddenly rotates 5 deg clockwise about its line of sight while the left eye stays put, then a line that was formerly seen single will now be seen double, with 5 deg of torsional disparity. So torsional disparity of line images conveys an ambiguous message. Part of it reflects the tilt of the line relative to the head, but part of it reflects the relative tilt of the eyes.

There is a special case, however, where the message is clear and unambiguous. When the line is in the visual plane, the torsional disparity of its images depends only on the relative cyclotorsion of the two eyes (cf. Rogers & Howard, 1991). If the eyes have the same Helmholtz torsion, the line will be seen singly. If not, the torsional disparity of the line will equal the difference between the Helmholtz-torsional angles (except for possible small imprecisions discussed in the Appendix, under *Helmholtz torsion and the visual plane*). In other words, the misalignment of the images of the visual plane reveals how strongly ocular tilt is contributing to the torsional disparities throughout the visual field. To reconstruct the 3-D geometry of the visual world, the brain must effectively remove this contribution from all torsional disparities. By aligning the images of the visual plane, L2 nulls this torsional bias with eye movements, setting it to zero at the outset so that later visual processors do not have to deal with it. With the bias removed, it may then be easier for the brain to interpret the remaining disparity of other lines. That is, by eliminating disparity of the visual plane, L2 may simplify spatial perception.

A potential problem with this notion is that it applies only when $\mu = \frac{1}{4}$. If μ is close to but not exactly equal to $\frac{1}{4}$, then the torsional disparity of the images of the visual plane is not eliminated but merely reduced (relative to what it would have been with $\mu = 0$) and if this torsional bias is still present, the value of the whole strategy becomes less clear. One possible resolution is that the reduced bias is brought "close enough" to zero to simplify subsequent visual processing. Given the "error tolerance" of the visual system, as reflected, for example, in the existence of Panum's fusional area, perfect zeroing may not be necessary. Another possibility is that μ does equal $\frac{1}{4}$ in normal life, but falls away from that level during some experiments, in much the same way that the gain of the vestibulo-ocular reflex, or VOR, falls away from its ideal behaviour. When an alert subject rotates horizontally in a lighted room, the VOR performs well, counter-rotating the eyes with a velocity equal and opposite to head velocity. But when the lights go out or the subject becomes bored, the eye movements slow down, presumably to save muscle energy. Similarly, our binocular control system may keep $\mu = \frac{1}{4}$ when our visual surroundings excite us, but may allow μ to dwindle or drift in the impoverished visual world of some labs.

Head tilts

As all current data on 3-D binocular coordination come from studies where the subject's head was fixed, it remains to be seen how precisely L2 holds when the head moves. We know already that it will not hold exactly in its head-fixed form, because Listing's law, which is one of its consequences, does not hold exactly: Listing's plane fails to stay fixed in the head, but countertilts slightly when the head tilts relative to gravity (Haslwanter *et al.*, 1992; Straumann *et al.*, 1991). Can the visual-motor theory accommodate tilting planes? There is no major problem, if we take the centre-court principle (see *A motor theory*, above) as the main underlying reason for minimizing eye eccentricity. On this view, the orientation of Listing's plane depends on the location of "visual centre court", and we can plausibly suppose that the brain's definition of centre court shifts when the head tilts: it moves slightly up, relative to the head, when the head is bowed, and it moves down when the head is raised, so as to stay nearer the horizon plane, closer to where most of the interesting visual events take place.

Prism adaptation

If the visual-motor theory is correct, then altering binocular correspondence should induce motor adaptation that realigns the images of the visual plane while minimizing eye eccentricity. For example, placing a base-down prism in front of the right eye causes, to a good approximation, an upward vertical rotation, through some angle j, of the visual scene projected onto that eye. If the left eye is pointing straight-ahead, in its primary position, then the right eye could simply "verge" upward through angle j, if the only concern were to get both foveae on target. However, the visual-motor theory predicts that both eyes will alter their vertical and torsional motion patterns so as to minimize eccentricity and better align the images of the visual plane.

The motion pattern predicted by the original, unextended visual-motor theory is shown in the simulation in Fig. 5: the primary plane of the right eye tilts down and that of the left tilts up; (the predictions of the extended theory are similar, except that the tilt angles can be smaller). Note that the directions of tilt are somewhat surprising. The right eye "verges" downward to achieve fusion through the prism, and its primary plane is predicted also to tilt down, whereas during normal, horizontal vergence (as described above in the definition of L2) the primary planes turn temporally, opposite vergence. To date, experiments with such prisms have involved exposures too brief for complete adaptation. Straumann & Müller (1994) placed a base-up prism

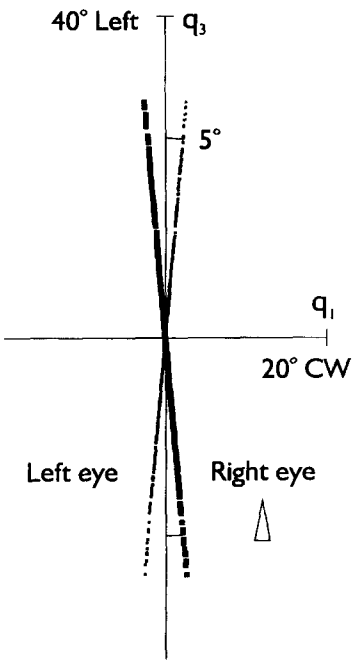

FIGURE 5. The visual-motor theory predicts that the primary planes of both eyes will tilt vertically when a prism is worn before one eye. This computer simulation minimizes eye eccentricity [Eq. (7)] while holding the Helmholtz-torsional coordinates of the two eyes equal [Eq. (5)]; i.e., it implements the original visual-motor theory, VM. Quaternion vectors of eye position are seen from the subject's right side, so that the torsional and horizontal components q_1 and q_3 are seen. The primary plane of the right eye tilts 5 deg up while that of the left eye tilts 5 deg down. Results for the extended theory VM* are similar, except that the angles of plane tilt can be smaller.

before one eye and a base-down prism before the other, while Mikhael *et al.* (1994) had subjects wear a prism over one eye for 15–30 min. The latter group reported that primary planes tilted vertically in the directions predicted here, but the results were noisy, and both studies found horizontal rotations that are not predicted by the visual-motor theory. Moreover, these unexpected horizontal turns were in opposite directions in the studies by the two groups. Presumably, after 0–30 min of experience with a vertical prism, the subjects' oculomotor systems were still groping for a solution to a bizarre visual situation. The prediction of the visual-motor theory is that after a sufficient adaptation period, say 6–8 hr, the responses will settle to the pattern shown in Fig. 5.

Models

The saccade/vergence model in Fig. 3 [and Eq. (8)] is expressed in Helmholtz coordinates, while that in Fig. 4 [and Eq. (11)] operates in the closely related T^* coordinates defined in Eq. (9). Both models steer the two eyes with the minimum possible number of channels, namely three. Signals V_C and H_C can be regarded as belonging to the conjugate saccadic system, and to the pursuit system as well if this obeys L2, whereas D arises from a separate vergence system. Thus, for example, H_C and D might correspond to the conjugate and disconjugate channels in the horizontal version–vergence model of Zee *et al.* (1992).

However, assigning just two channels, H_C and V_C, to the saccadic and pursuit systems is probably unrealistic. It is known that the final output path of the saccadic system is three-dimensional, with three roughly orthogonal populations of burst neurons, tonic cells and motoneurons (Crawford *et al.*, 1991; Henn *et al.*, 1989; Hepp *et al.*, 1994; Vilis *et al.*, 1989). Of course, the system may nevertheless be two-dimensional at higher levels, but even that is doubtful. Outputs of the superior colliculus appear to be roughly two-dimensional (Van Opstal *et al.*, 1991; although see Van Opstal & Hepp, 1995) but it has recently been shown that the colliculus drives both eye and head motion in monkeys, and its activity correlates better with the motion of the gaze line in space than with the motion of the eye in the head (Robinson & Cowie, 1994). That is, the superior colliculus appears to code the direction of the visual target rather than the desired saccade of the eye in the head. Downstream from colliculus, in the eye saccadic system proper, the signals seem to be three-dimensional. For example, it has long been known that quick phases of nystagmus have three degrees of freedom, and so this kind of "saccade" cannot be generated by a two-dimensional controller. In addition, recently it has been found that the eye movement component of an eye–head saccade can carry the eye out of Listing's plane even before the head begins to move (Tweed, 1995; Tweed *et al.*, 1995), strongly suggesting that the desired position or movement command driving the eye has three degrees of freedom. In short, the immediate premotor circuitry driving saccades may operate two-dimensionally when the head is held fixed, but under natural conditions, an additional torsional dimension is revealed (Tweed *et al.*, 1995). Similarly, our ability to verge torsionally and vertically in certain situations, such as when looking through prisms (see section entitled: *Prism adaptation*, above), shows that, somewhere in its circuitry, the disconjugate system has access to more than one degree of freedom, and so the models in Figs 3 and 4 can only hope to mimic the normal, default control of vergence.

Although, for simplicity, the flow diagrams in Figs 3 and 4 were drawn showing only position commands, in reality there must of course be velocity commands as well, and it may be at the level of the velocity variables that the torsional commands are computed. For instance the signal T_R^*, which in Fig. 4 is computed by multiplying two position signals, D and V_C, and scaling by μ, could also be obtained by integrating a torsional velocity command $\dot{T}_R^*$, computed from vertical and disconjugate velocity signals by the equation $\mu(\dot{D}\,V_C + \dot{D}\,V_C)$. To test the models in Figs 3 and 4, and their "velocitized" versions, electrophysiologically would involve looking for neural signals correlated with the eyes' Helmholtz or T^* coordinates, and the derivatives of those coordinates, in burst, burst-tonic and motoneurons. Given the oblique arrangement of the eyes' vertical muscles, it is very unlikely that motoneurons will be found to carry signals

coding the Helmholtz vertical or torsional angles of the eye, but it is possible that different pools of motoneurons carry signals related to H, $V + T$ and $V - T$, or H, $V + T^*$ and $V - T^*$.

How might the output position commands of the two models be converted into extraocular muscle activity? If the muscles behaved like a set of Helmholtz gimbals then the output signals in Fig. 3—V_R, V_L, H_R, H_L, T_R and T_L—could be sent directly to the motoneurons. But as noted above, it is very improbable that the muscles behave this way. More likely, some sort of neural version of a device driver would be required to interface with the muscles, although this driver might not require an extra layer of neurons, but could be implemented by the pattern of projections from Helmholtz-coordinate neurons to motoneurons. Plausible three-dimensional plant models can be built that are driven in a simple way by signals in Helmholtz or T^* coordinates, but too little is known about the three-dimensional properties of the ocular plant to provide much support for any quantitative specification right now.

Visual-motor geometry

According to the visual-motor theory developed here, the brain system that steers the two eyes optimizes a mixture of visual and motor variables. It strives to keep the images of the visual plane as nearly aligned as possible in the two eyes, and also to cyclorotate the eyes about their own lines of sight so as to keep them as close as possible to their zero-vergence primary positions. The balance between these incompatible goals determines the pattern of eye positions seen during fixation of targets anywhere in space.

The main results and predictions in this paper are: (1) Because of the tilt of the vertical horopter, keeping the Helmholtz-torsional coordinates of the two eyes equal will not ensure single vision of lines orthogonal to the visual plane, but it will eliminate cyclodisparity of the plane itself. (2) The two eyes are predicted to rotate about different axes and at different speeds when saccading or pursuing a target across a close isovergence surface. If so, then the eyes are *not* driven solely by a common angular velocity signal during this task. (3) If the visual-motor theory, proposed here as an explanation for L2, is correct then placing a vertical prism in front of one eye will evoke adaptive changes in the motion of both eyes, so that their primary planes tilt vertically and symmetrically. (4) L2 is compatible with a simple control system, with one eye position channel devoted to vergence and two to head-fixed, conjugate saccades and pursuit. Equations (8) and (11) define two possible models, and also offer simple formulae for mimicking human binocular coordination in robots and stereopsis simulations.

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APPENDIX

Vertical horopter

For the simulation in Fig. 1, we initially place both eyes in their primary positions and assume that the two gaze lines are parallel and straight-ahead. We construct a parasagittal plane through the centre and nodal point of each eye, and then excyclorotate each plane by 1 deg, turning the right eye plane clockwise and the left eye plane counterclockwise, so that the arcs where the planes intersect their respective retinas will be corresponding lines, which tilt ~2 deg relative to one another (Ogle, 1950). Call these "corresponding planes" C_R and C_L. Unit normal vectors to these planes are:

$$N_R = (0, \cos 1^\circ, \sin 1^\circ), N_L = (0, \cos 1^\circ, -\sin 1^\circ) \quad \text{(A1)}$$

When the eyes are away from their primary positions, C_R and C_L will be rotated into new orientations, C_R' and C_L'. If q_R and q_L are the quaternions of right and left eye position, then the new orientations of the normal vectors are given by quaternion conjugation; i.e.

$$N_R' = q_R N_R q_R^{-1}, \; N_L' = q_L N_L q_L^{-1} \quad \text{(A2)}$$

If the eyes are converged, the planes C_R' and C_L' must intersect somewhere in space. The line of their intersection is the vertical horopter L. Because it lies in both C_R' and C_L', L must be orthogonal to both normal vectors; i.e., L is obtained by normalizing the cross product:

$$N_R' \times N_L' \quad \text{(A3)}$$

For the simulation in Fig. 1, 20 fixation points f were selected, and binocular configurations fitting L2 with $\mu = \frac{1}{4}$ were computed using Eq. (8). Specifically, the vertical angle of f [which corresponds to V in Eq. (8)] varied from 45 deg up to 45 deg down in 22.5-deg steps; the conjugate horizontal angle H was 0 because all fixation points were chosen to lie in the sagittal plane of the head; and vergence, D, was set at 3, 5, 9 and 15 deg. From these V, H and D values, Eq. (8) then yielded the Helmholtz coordinates of the two eyes. These coordinates were converted to quaternions using Eq. (2), and the latter were applied to find L using Eqs (A1)–(A3).

Helmholtz torsion and the visual plane

It is easily proven that, if the Helmholtz-torsional coordinates of the two eyes are equal to zero, then the visual plane will cast its images on the horizontal meridians of both retinas. Given that these meridians are corresponding lines, or at least extremely close to corresponding (Helmholtz, 1867), it follows that the visual plane will be seen without cyclodisparity. (Note that this does not mean that all points in the visual plane are seen single, but that all lines in the plane, as well as the plane as a whole, are seen without cyclodisparity. That is, the images on the two retinas of this plane and its contained lines are not tilted relative to one another.)

However, Eq. (5) does not state that the Helmholtz-torsional angles of the two eyes are zero, but merely that they are equal to each other. Thus, if the two eyes have a Helmholtz-torsional angle of T deg clockwise, then the visual plane will cast its images on the oblique meridians, rotated T deg *counter*clockwise (with respect to the retina) from the horizontal meridian. Are these oblique meridians corresponding lines? Clearly not for all values of T, because if $T = 90$ then the meridians in question are the vertical ones, which we know are not corresponding lines (Helmholtz, 1867; see also Fig. 1). Fortunately, we only require that the assumption holds for $T \leq 20$, because the visual-motor strategy keeps Helmholtz torsion smaller than 20 deg within the oculomotor range. That is, if we apply Eq. (8) and assume that the maximum horizontal and vertical angles H and V are 45 deg, then the maximum possible value for T_R or T_L is $-2\tan^{-1}(\tan(22.5)\tan(22.5)) \approx 19.5$ deg. To my knowledge, correspondence of oblique meridians has never been carefully measured. Because the meridians in question are close to the horizontal, the best assumption is probably that they are close to being corresponding lines. However, it remains an open question whether there are small deviations, and whether the eyes violate Eq. (5) to correct for such deviations.

Visual-motor simulations

The simulation in Fig. 2(A) was presented with 500 fixation points on a 40-deg isovergence surface, and computed the binocular configuration for each fixation that satisfied Eq. (5) and minimized the cost function in Eq. (6). To specify each fixation point, the simulation program chose a vertical angle V and a horizontal angle H pseudorandomly and independently from a ± 30-deg range. By Eq. (1), binocular foveation requires that the Helmholtz vertical coordinates of the two eyes be equal, so V_R and V_L were set equal to V. The horizontal coordinates were set at $H_R = H + 20$ deg, $H_L = H - 20$ deg. These vertical and horizontal coordinates ensured that both gaze lines were aimed at the same target, with 40 deg of vergence. The task was then to find a common Helmholtz-torsional angle $T = T_R = T_L$ for the two eyes [thus satisfying Eq. (5)] such that the cost function in Eq. (7) was minimized. This torsion angle was found simply by stepping from $T = -90$ deg to +90 deg in 0.1 deg increments and storing the torsion angle that yielded the smallest value of the cost function [Eq. (6), using

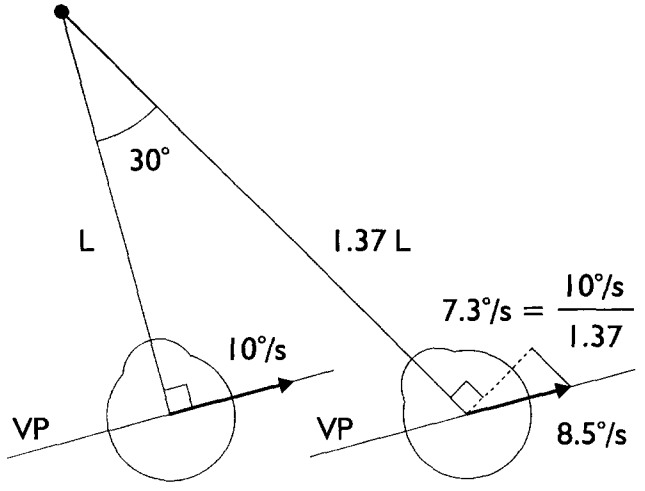

FIGURE A1. To obey L2 with $\mu = \frac{1}{4}$, the right eye must rotate only 0.85 as fast as the left when pursuing a target moving upward on a 30 deg isovergence surface. See Appendix: *Binocular pursuit*.

the formula for ε from Eq. (4)]. With the V, H and T coordinates in hand, the quaternion vectors for the two eyes were computed using Eq. (2) and the torsional and vertical components (i.e., q_2 and q_2) were plotted in Fig. 2(A).

For the simulation in Fig. 2(B), the condition that $T_R = T_L$ was dropped. Horizontal and vertical Helmholtz coordinates of the two eyes were chosen as for Fig. 2(A), but then the program used gradient descent to find the *pair* of torsion angles (T_R, T_L) that minimized the cost function in Eq. (7), with the weighting factor α set equal to 3.

Figure 5 simulates the pattern of eye positions predicted after adaptation to a base-down prism in front of the right eye, causing the right visual field to rotate 20 deg down. The condition that $T_R = T_L$ was restored for this simulation, but Eq. (1) was replaced by the requirement that $V_R = V_L - 20$ deg; (horizontal) vergence was set at 0 deg. As in Fig. 2(A), the torsion angle minimizing the cost function in Eq. (6) was found by a simple one-dimensional search.

Binocular pursuit

This section deals with the consequences of L2 for the velocity commands driving the two eyes. Pursuit movements are considered because they are directly concerned with eye velocity, but if it is found that pursuit does not obey L2 the conclusions obtained will still apply to saccades. Figure A1 shows a situation where the two eyes must pursue at different speeds to obey L2. Two eyes, seen from above, are converged 30 deg on a point target (the black dot) in the horizontal plane. At the instant shown in the picture, we suppose that the target is moving straight upward, orthogonal to the page. This vertical velocity lies in the tangent plane to the 30 deg isovergence surface, so this instantaneous velocity vector is compatible with a target motion confined to the surface. When the two eyes are in the positions shown and are pursuing a target moving on an isovergence surface, L2 ($\mu = \frac{1}{4}$) requires that the velocity planes (VP) of the two eyes (i.e., the planes containing the angular velocity vectors) be parallel and rotated 15 deg left as shown (see Mok *et al.*, 1992). The arrow on the left depicts the angular velocity vector of the left eye, whose magnitude is 10 deg/sec. Note that this velocity vector is orthogonal to the gaze line.

What is the right eye's velocity? To start with, note that the path from the target to the nodal point of the eye (assumed, for simplicity, to coincide with the rotational centre) is 1.37 times longer for the right eye than for the left. This means that if the right eye were permitted to rotate about an axis orthogonal to its gaze line, it would only need to rotate 1/1.37 = 0.73 times as fast as the left eye, i.e., at 7.3 deg/sec, to track the target. However, the orthogonal axis (dashed line) is not a permissible axis because it does not lie in VP. To find the actual eye velocity, we must project the dashed vector along the line of sight onto VP (for an explanation of velocity projection, see Misslisch *et al.*, 1994, or Tweed *et al.*, 1992). The result, shown as a solid arrow, is only 0.85 times as large as the velocity vector of the left eye, yielding a speed of 8.5 deg/sec. Thus, the two eyes must rotate at different speeds to match the instantaneous velocity of the target and obey L2. And by less picturesque, more algebraic methods it is possible to prove that the two eyes must not only have different speeds but also different *axes* of rotation.